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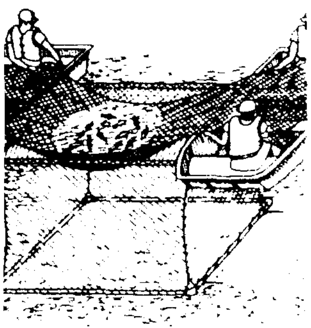

AQUATIC PLANT CONTROL
RESEARCH PROGRAM

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HABITAT VALUE OF AQUATIC PLANTS FOR FISHES

by

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The habitat value of submersed aquatic plants (*Myriophyllum spicatum* and *Hydrilla verticillata*) for fishes was determined from field studies conducted at four locations in the United States. Seasonal distribution and relative abundance was evaluated at the Potomac River near Washington, DC, by sampling fish with an electroshocking boat at night in May (plant emergence), August (peak plant biomass), and November (plant senescence). The density of fishes in submersed aquatic plants was measured with popnets at the Potomac River, Lake Seminole, Florida-Georgia, Lake Guntersville, Alabama, and Pend Orielle River, Washington. Feeding habits of fishes were compared between vegetated and nonvegetated areas at Lake Seminole.

The seasonal distribution and relative abundance (catch per 5-min shocking) of fishes were estimated in three densities of submersed aquatic plants (no plants, intermediate plant density, high plant density). *Hydrilla verticillata* was usually the dominant aquatic plant. In May, mean fish abundance was highest in areas of high plant density, whereas in August and November fish

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abundance was highest in areas of intermediate plant densities. Areas without plants were numerically dominated by filter-feeding fishes including Atlantic menhaden and blueback herring. The fish assemblage in the vegetated sites was comprised mainly of brown bullhead, banded killifish, pumpkinseed, largemouth bass, and yellow perch. The bay anchovy, white perch, and inland silverside were equitably distributed throughout all three sites during the study.

Popnets were used in a range of plant densities (0-1,000 g/m^2) and water depths (0.91-3.05 m) at each site to estimate number of fishes within the plant community. Popnets were set in *Myriophyllum spicatum* at Lake Guntersville and Pend Orielle River, and in *Hydrillia verticillata* at the Potomac River and Lake Seminole. Geographical differences in fish density and species composition was pronounced. Mean density (number/10 m^2) of all species combined ranged from 5.1 ± 3.6 at the Pend Orielle River to 204.1 ± 62.8 at Lake Guntersville. Popnets caught a significantly ($P<0.05$) higher number of fishes at Lake Guntersville than at the other three locations. Species richness ranged from 7 species at the Pend Orielle to 11 species at Lake Seminole and the Potomac River. Most collections at all four sites were dominated by juvenile centrarchids. Fish densities within a site were variable, suggesting patchy distributions of fishes possibly caused by diel changes in water quality or segregation between distinct habitats formed by large plant beds (i.e., the water surface immediately above the plants, the periphery or edge of the dense stands, "holes" formed in the plant beds, or the bottom directly below dense canopy formations).

Food habits were determined for 10 abundant species: coastal shiner, golden topminnow, eastern starhead topminnow, bluefin killifish, least killifish, brook silverside, bluespotted sunfish, bluegill, redear sunfish, and largemouth bass. The 10 fishes studied represented several trophic guilds, although no species was exclusively herbivorous. Fishes fed chiefly on hydracarina, detritus, larval chironomids, and filamentous algae. Our results suggest that diet shifts can be substantial between habitats (i.e., dissimilarity > 40 percent) within an entire assemblage, irrespective of trophic guilds and degree of dietary specialization. Substantial habitat-associated differences in diet existed for all species, suggesting that differences in diet composition were largely attributable to differences in invertebrate availabilities rather than structure-induced changes in feeding behavior or feeding efficiencies.

Contents

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP). The APCRP is sponsored by Headquarters, US Army Corps of Engineers (HQUSACE), and is assigned to the US Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation 96X3122 Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel was Assistant Manager, ERRAP, for the APCRP. Technical Monitor during this study was Mr. James W. Wolcott, HQUSACE.

This report was prepared by Mr. K. Jack Killgore, Aquatic Habitat Group (AHG), Environmental Resources Division (ERD), EL, WES, and Drs. Jan Jeffrey Hoover and Raymond P. Morgan II, University of Maryland, Center for Environmental and Estuarine Studies, Appalachian Environmental Laboratory. Assistance in field sampling was provided by Andrew Miller, Ken Conley, and Frank Ferguson, WES. Assistance was also provided by personnel from the US Park Service, US Geological Survey, US Fish and Wildlife Service, Georgia Department of Natural Resources, University of Maryland, Tennessee Valley Authority, Washington State Department of Ecology, University of Idaho, and Dr. Neil Douglas, Northeast Louisiana University.

The study was supervised at WES by Mr. Ed Theriot, Chief, AHG, EL, and Dr. Conrad J. Kirby, Chief, ERD, EL. Dr. John Harrision was Chief, EL.

Commander and Director of WES was COL Larry B. Fulton, EN. Technical Director was Dr. Robert W. Whalin.

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1 Introduction

Background

Aquatic plants are conspicuous features of many waterbodies in the United States and the fishes associated with them have been documented in numerous studies. Some species of fish (e.g., sunfish, bullheads) are substantially more abundant in vegetation, while other species (e.g., shad, silversides) are more common in open water (Goin 1943; Swift, Yerger, and Parrish 1977; Laughlin and Werner 1980; Holland and Huston 1984). These disparities in abundance have allowed distinctive fish assemblages to be quantitatively described for vegetated and open-water habitats (Barnett 1972; Guillory, Jones, Rebel 1979; Killgore, Morgan, and Rybicki 1989; Werner, Hall, and Werner 1978).

Submersed aquatic plants influence both fish distribution and abundance by creating structurally complex habitats (Crowder and Cooper 1979) that affect predator-prey relationships (Barnett and Schneider 1974; Moxley and Langford 1982). Total fish abundance can be substantially higher in areas with aquatic plants than in areas without plants (Laughlin and Werner 1980; Holland and Huston 1984). However, foraging success of predators generally declines as plant density increases (Reynolds and Babb 1978; Savino and Stein 1982; Durocher, Provine, and Kraai 1984; Wiley et al. 1984). Although aquatic plants are an important component of aquatic ecosystems, their effect on the environment has not been well documented (Carpenter and Lodge 1986).

Purpose and Scope

This paper describes the value of submersed aquatic plants to fishes based on field studies conducted in reservoirs and rivers colonized by hydrilla (*Hydrilla verticillata*) or Eurasian watermilfoil (*Myriophyllum spicatum*). Information is provided on seasonal distribution and relative abundance, density, and feeding habits of fishes associated with submersed aquatic plants.

Field studies were conducted at four locations in the United States (Figure 1): Potomac River near Washington, DC, Lake Guntersville, Alabama, Lake Seminole, Georgia-Florida, and Pend Orielle River, Washington. Seasonal distribution and relative abundance of fishes were evaluated at the Potomac River in 1986. Relationships between fish and plant density were measured once at all four locations from 1986-1989. The food habitats of fishes associated with aquatic plants were determined at Lake Seminole in 1988.

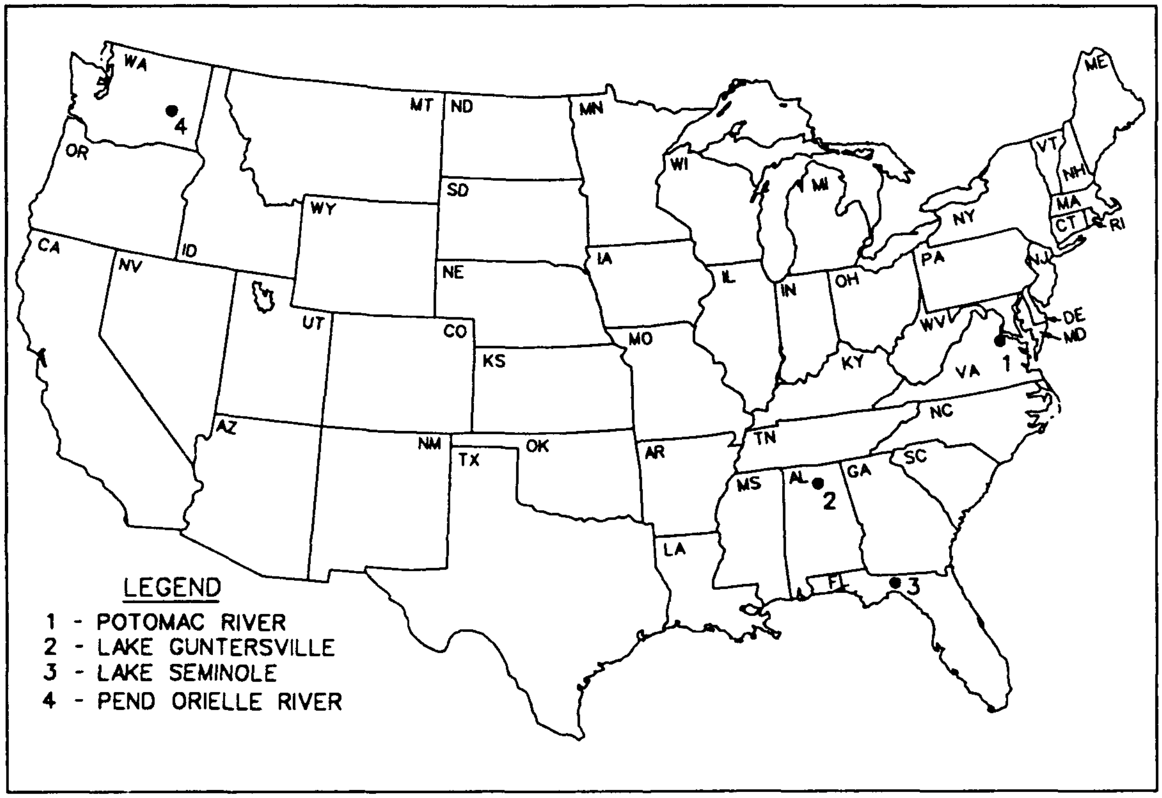


Figure 1. Location of field sites

2 Description of Study Sites

Potomac River

The study area was located in the tidal Potomac River between Woodrow Wilson Bridge (166 river km) and Gunston Cove (140 river km) near Alexandria, VA. The water is usually fresh (<0.5 ppt salinity) and the 51-year average annual freshwater inflow is 323 m^3/sec (Callender et al. 1984). The tidal area is shallow with an average depth of 6 m; depths vary about 1 m with the tide. The channel is flanked on one or both sides by wide shallow flats. In 1983, 12 species of submersed aquatic plants were present in the tidal Potomac River; plants had been rare in this part of the river since the late 1930's. In 1984, approximately 242 ha were colonized by plants. In 1985, coverage increased to 1,456 ha and remained about the same in 1986 (Rybicki et al. 1987). Plant species include hydrilla, eelgrass (*Vallisneria americana*), Eurasian watermilfoil, water stargrass (*Heteranthera dubia*), coontail (*Ceratophyllum demersum*), southern naiad (*Najas guadalupensis*), common naid (*Najas minor*), and stonewort (*Nitella flexilis*). Hydrilla dominates the plant community it occupies and becomes very dense during the summer and early fall in water depths less than 2 m. On the periphery of these dense beds, plants occur in patches to a depth of approximately 3.0 m.

Lake Gunterville

Lake Guntersville is a reservoir that was formed by the impoundment of the Tennessee River in 1939. It is 122 km long with a surface area at maximum pool level of 27,479 ha, a maximum depth of 18 m at the dam, a mean depth of 4.6 m, and a high reservoir flushing rate (mean 13 days) (Poppe 1987). Approximately 3,316 ha of aquatic plants occurred in the reservoir in 1988; dominant species in decreasing order of abundance were Eurasian watermilfoil, hydrilla, and spinyleaf naid (Burns, Bates, and Webb 1989). Fishes were collected at Conners Island located next to the main channel of the Tennessee River immediately north of Highway 79 Bridge (10 km upstream from the dam). Water depth at the collecting

site ranged from 1-3 m. Eurasian watermilfoil was the dominant plant species at all collecting sites.

Lake Seminole

Lake Seminole is a reservoir formed by the impoundment of the Chattahoochee and Flint rivers on the Georgia-Florida border. The impoundment provides for hydroelectric generation, flood control, and recreation. It has a total watershed of 4.5 million ha and a surface area at maximum pool level of 15,182 ha (US Army Corps of Engineers 1974). Mean depth is 3 m and maximum depth is 10.7 m. A variety of aquatic plants occurs in the reservoir but hydrilla and Eurasian watermilfoil dominate most of the littoral zones. Fishes were collected 14-15 July 1987 from two stations in Fish Pond Drain, a cove of Lake Seminole; one station was densely vegetated, the other was not. The average depth at both sites was approximately 1.5 m. The station with aquatic plants was dominated by hydrilla, with some growths of Illinois pondweed (*Potamogeton nodosus*) and water lily (*Nuphar luteum*). The nonvegetated station was located adjacent to Seminole State Park approximately 2 km from the vegetated station. This site had no conspicuous growth of aquatic plants, except for musk-grass (*Chara* sp.) occurring in patches along the bottom.

Pend Orielle River

The Pend Orielle River is located in northeastern Washington and flows north into British Columbia where it empties into the Columbia River in southern British Columbia. The drainage area is 64,750 square km and extends into Washington, Idaho, and Montana. The mean daily discharge recorded at Newport, WA (river km 229) is 737 cms. Eurasian watermilfoil is the dominant aquatic plant and grows parallel to the river bank but can also form large beds on shallow flats. The presence of curlyleaf pondweed (*Potamogeton crispus*), elodea (*Elodea canadensis*), and American milfoil (*Myriophllum exalbescens*) form mixed plant communities with Eurasian watermilfoil. Fishes were collected 15-17 Aug 1989 at river km 108 near Usk, WA, in water depths ranging from 1-3 m. Current was slow (<10 cm/s) and average depth at the collecting stations was approximately 2 m.

3 Methods

Seasonal Distribution and Relative Abundance

Study sites, which were sampled in May (plant emergence), August (peak biomass), and November (senescence) 1986, were chosen to represent three relative levels of aquatic plant density in the Potomac River: no plants (NP), intermediate plant density (IPD), and high plant density (HPD). In May, the HPD site consisted largely of Eurasian watermilfoil, whereas the IPD site contained hydrilla sprouts just emerging from tubers and turions. By August, the hydrilla at the IPD site had spread along the bottom and lengthened vertically to completely fill the water column. Therefore, new sites were chosen in August and these sites remained the same for the November collections. At these times, hydrilla and Eurasian watermilfoil were the dominant plant species at the HPD and IPD sites, respectively.

Plant biomass was quantified by collecting 10 plant samples at each site. A 930 cm^2 frame was randomly placed over the plants and on the bottom by SCUBA divers. Divers would collect all aboveground plants within the frame. Dry weight was determined for each sample. Seasonal plant density ranged from 9 g/m^2 in May to 728 g/m^2 in November at the IPD site and 33 g/m^2 in May to 1,043 g/m^2 in August at the HPD site.

On each sampling date and at each site, replicate fish samples were collected at night (1-3 hr after sunset) using a boat-mounted electroshocker with two netters on the bow. One replicate consisted of 5 min of continuous shocking. The electroshocker provided a constant output of 300-400 V at 4-7 A. All collected fishes were identified by species and total length was measured to the nearest millimeter.

An analysis of variance (ANOVA) and Duncan's multiple range test (SAS Institute 1985) were used to determine the influence of plant density on the fish assemblage at each stage in the life cycle of the plants. The dependent variables analyzed were species richness (total number of species), fish length, abundance (number of fishes captured per 5 min of shocking and number per unit area) of the fish community, and abundance of individual fish species.

Density

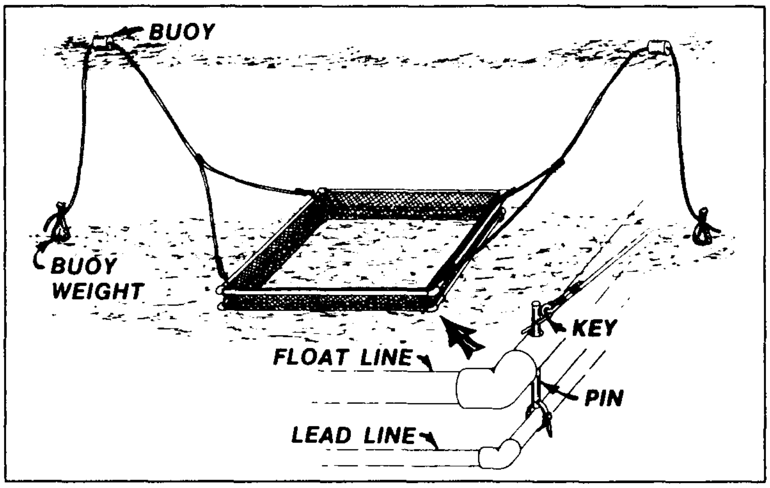
Popnets described by Morgan, Killgore, and Douglas (1988) were used to estimate fish density in submersed aquatic plants (Figure 2). Nets were assembled onshore, placed on a large boat (>5 m), and deployed at each sampling location. Nets were set during midday and allowed to equilibrate until after dusk. The nets were released approximately 1 to 2 hr after dark, except for the Potomac river where nets were released during late afternoon. After the nets had been popped, a seine (Figure 2) was used to remove fishes. All fishes collected were identified, counted, and measured. A Zippin depletion method (Armour, Burnham, and Platts 1983) using three removals was used for the estimation of numbers of fishes.

Popnets were used in a range of plant densities (0-1,000 g/m^2) and water depths (1-3 m) at each of the four sites to estimate numbers of fishes within the plant community. Popnets were set in Eurasian watermilfoil at Lake Guntersville (9 nets) and Pend Orielle River (10 nets), and in hydrilla at Potomac River (6 nets) and Lake Seminole (4 nets). Plant biomass was quantified using the same techniques as the electroshocking data. Statistical comparisons of plant and fish densities were made using ANOVA and Duncan's multiple range test (SAS Institute 1985).

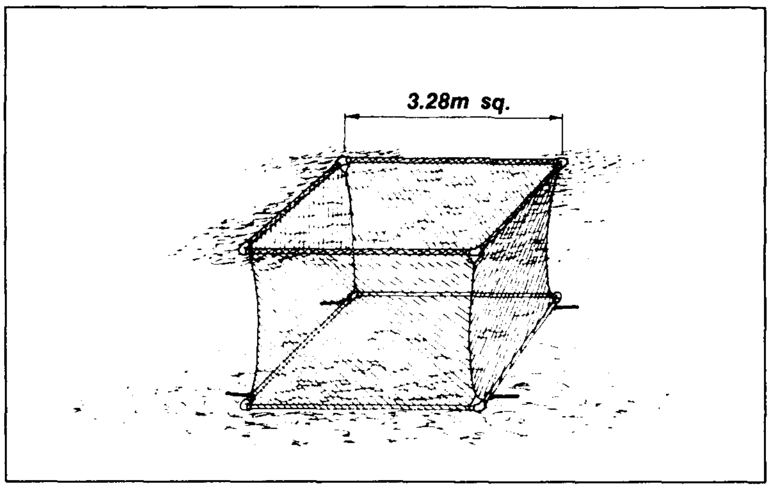
Feeding Habits of Fishes

Fishes were collected in Lake Seminole at vegetated and nonvegetated sites with seines and a boat-mounted electroshocker. Specimens were preserved in the field in a 10-percent formalin solution and later washed and transferred to a 55-percent isopropyl alcohol solution. Fishes were identified, counted, and total length measured to the nearest millimeter. Food habits were determined for 10 abundant species: coastal shiner, golden topminnow, eastern starhead topminnow, bluefin killifisn, least killifish, brook silverside, bluespotted sunfish, bluegill, redear sunfish, and largemouth bass. Table 1 lists the scientific names.

The gut of each fish was removed and examined under a dissecting microscope. The stomach or anterior loop of the gut was separated from the lower tract, bissected, fullness estimated, and food items removed. Prey were identified to the lowest practical taxon and counted; plant foods were recorded as a single prey item. In most cases, the sample size was 15 individual fish/species/site. This sample size was considered adequate since at least 80 percent of all prey taxa eaten by a species at a site were recorded after examining 10 individuals (sample size = 15, standard deviation = 2). For several species (golden topminnow, eastern starhead topminnow, least killifish, and bluespotted sunfish), fewer than 11 individuals were collected at one of the sites. However, these data are also presented because prey numbers were relatively high (i.e., 39-130)

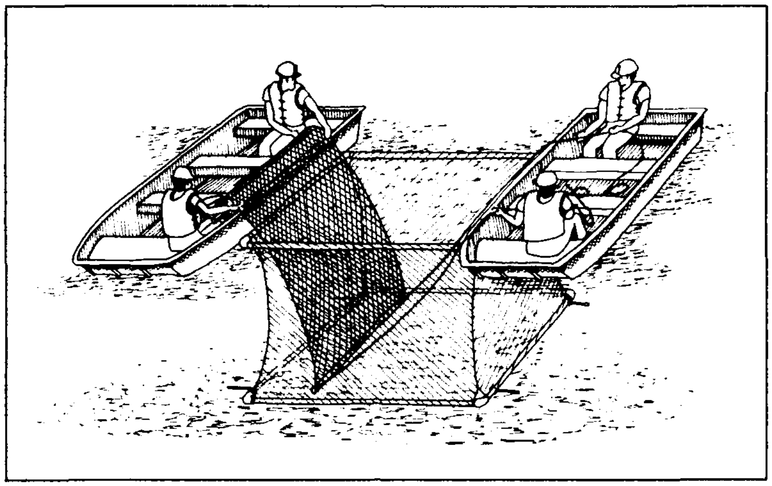


a. Popnet set on bottom–float and lead line attached with pin/key system

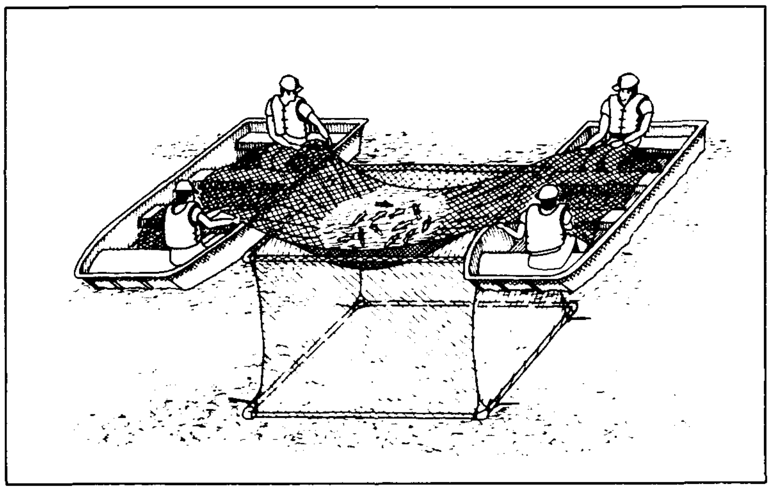


b. Popnet fully extended subsequent to release of floatline

Figure 2. Schematic of the popnet system (Continued)



c. Two boats positioned on opposite sides of popnet–seine lowered to bottom preparing to remove fish



d. Fish captured with seine after being pulled through popnet

Figure 2. (Concluded)

Table 1
Scientific Names of Fishes Collected

Family and Species	PR	LG	LS	POR
Lepisosteidae				
Longnose gar (*Lepisosteus osseus*)	X			
Anguillidae				
American eel (*Anguilla rostrata*)	X			
Clupeidae				
Blueback herring (*Alosa aestivalis*)	X			
Alewife (A. *pseudohargengus*)	X			
Atlantic menhaden (*Brevoortia tyrannus*)	X			
Gizzard shad (*Dorosoma cepedianum*)	X			
Engraulidae				
Bay anchovy (*Anchoa mitchilli*)	X			
Cyprinidae				
Tench (*Tinca tinca*)				X
Common carp (*Cyprinus carpio*)	X			
Goldfish (*Carrassius auratus*)	X			
Golden shiner (*Notemigonus crysocleucas*)	X	X		
Taillight shiner (*N. maculatus*)			X	
Spottail shiner (*N. hudsonius*)	X			
Coastal shiner (*N. petersoni*)			X	
Catostomidae				
White sucker (*Catostomus commersoni*)	X			
Longnose sucker (*Catostomus catostomus*)				X
Ictaluridae				
Black bullhead (*Ictalalurus melas*)		X		
Brown bullhead (*I. nebulosus*)	X			X
Channel catfish (*I. punctatus*)	X			
Belonidae				
Atlantic needlefish (*Strongylura marina*)	X			
Cyprinodontidae				
Golden topminnow (*Fundulus chrysotus*)			X	
Banded killifish (*F. diaphanus*)	X			
Mummichog (*F. heteroclitus*)	X			
Eastern starhead topminnow (*F. escambia*)			X	
Bluefin killifish (*Lucania goodei*)			X	
Poeciliidae				
Mosquitofish (*Gambusia affinis*)	X		X	
Least killifish (*Heterandria formosa*)			X	
Atherinidae				
Brook silverside (*Labidesthes sicculus*)		X	X	
Inland silverside (*Menidia beryllina*)	X			
Atlantic silverside (*M. menidia*)	X			

Notes:
PR - Potomac River (electroshocking and popnets)
LG - Lake Guntersville (popnets)
LS - Lake Seminole (popnets)
POR - Pend Orielle River (popnets)

Continued

Table 1 (Concluded)

Family and Species	PR	LG	LS	POR
Percichthyidae				
White perch (*Morone americana*)	X			
Striped bass (*M. saxatilis*)	X			
Centrarchidae				
Bluespotted sunfish (*Enneacanthus gloriosus*)	X		X	
Redbreast sunfish (*Lepomis auritus*)			X	
Pumpkinseed sunfish (*L. gibbosus*)	X			X
Warmouth (*L. gulosus*)		X		
Bluegill (*L. marochirus*)	X	X	X	
Longear sunfish (*L. megalotis*)	X	X		
Redear sunfish (*L. microlophus*)		X	X	
Largemouth bass (*M. salmoides*)	X	X	X	X
Black crappie (*P. nigromaculatus*)	X			X
Percidae				
Tessellated darter (*Etheostoma olmstedi*)	X			
Yellow perch (*Perca flavescens*)	X			X
Sciaenidae				
Freshwater drum (*Aplodinotus grunniens*)		X		
Spot (*Leiostomus xanthurus*)	X			

and the food habits of these four species have received little attention from fish ecologists (Hunt 1952, Breder and Redmond 1929, Flemer and Woolcott 1966, Reimer 1970).

Diets were described based on mean number of prey and were compared within species between habitats and among species within habitats. Similarity of diet was quantified using the Percent Similarity Index (PSI) values for this index range from 0.000 (diets completely distinct) to 1.000 (diets completely identical) and are believed to provide the best estimates of "real" overlap (Linton, Davies, Wronga 1981).

Food habits for each species were ordinated by Principal Component Analysis (PCA) using ORDIFLEX (Gauch 1977). Ordinations were performed within fish species using individual fish as "samples" and prey taxa as "species" and plotting each fish in multivariate prey space. Only the first two principal components (PC) were considered in this study; for 9 of the 10 fishes, PCI and PCII accounted for a substantial percentage (50 percent and greater) of data set variance, and for the tenth species (bluegill) additional PC axes (PCIII, PCIV, PCV) did not account for a comparable cumulative variance (42 percent). Coordinates of all individuals of a species from each site were used to generate 95 percent confidence ellipses (Sokal and Rohlf 1981); this allowed simultaneous evaluations of diet shifts between sites (i.e., degree of spatial separation between two ellipses) and variability in food habits within a site (i.e., relative size of each ellipse). Stepwise regressions (Wolfe and Koelling 1984) of prey numbers and principal component scores were used to identify factors (prey taxa) significantly correlated with Principal Components I and II.

4 Results

Seasonal Distribution and Relative Abundance

There were significant differences ($P<0.05$) in overall mean number of fishes collected per 5-min shocking (CPUE) among sites at the Potomac River during the three sampling months (Table 2). The CPUE at the IPD site was the lowest among the three site types in May but the highest in November. Significantly more fish were collected at the HPD site than at the NP site in November. Mean lengths of fishes were usually lower at the NP site than at the two sites with vegetation. Between the vegetated sites, mean lengths were significantly higher at the HPD site in August and at the IPD site in November.

Thirty-one species were collected by electroshocking during the period of study (Table 1). More species were collected in areas with aquatic plants (18-23 species) than in areas devoid of plants (9-13 species). Except in May, the mean number of species collected per 5-min shocking was significantly ($P<0.05$) higher in vegetated sites than nonvegetated sites (Table 2). In May, species richness was highest in the HPD site followed by the NP and IPD sites. In August and November, however, species richness was not significantly different between the two vegetated sites, though it was at least two times higher than the NP site.

Fourteen species accounted for 90 percent of the total individuals collected (Table 3). In decreasing abundance, these included bay anchovy, white perch, inland silverside, largemouth bass, alewife, Atlantic menhaden, pumpkinseed, brown bullhead, banded killifish, yellow perch, spottail shiner, golden shiner, and bluegill. Of these species, those that were collected only in areas with plants were the golden shiner, bluegill, and yellow perch (Table 3). However, other species were captured in consistently low numbers in areas without plants including the alewife, spottail shiner, brown bullhead, banded killifish, pumpkinseed, and largemouth bass. Only the Atlantic menhaden appeared to prefer areas without vegetation. Species that were common in all three densities of vegetation were the bay anchovy, inland silverside, and white perch. Species with significantly higher ($P<0.05$) CPUE values at the NP site were the Atlantic menhaden (May and August) and bay anchovy (May) (Table 3). Species

Table 2
Mean (±SD) Catches of Fishes per 5-min Electroshocking (CPUE), Mean (±SD) Lengths of Captured Fishes, Number of Fishes Caught in Five Electrofishing Samples (N), and Mean (±SD) Numbers of Species Caught per Unit Effort in Relation to Plant Density in the Potomac River, 1986

Month and Variable	NP	IPD	HPD
May 1986			
CPUE	26.0 ± 12.8^z	2.0 ± 3.4^y	35.6 ± 23.3^z
Length	81.3 ± 77.1^z	143.2 ± 105.3^y	132.4 ± 79.2^y
N	130	12	178
Species	4.6 ± 0.9^z	1.4 ± 2.1^y	8.2 ± 1.9^x
August 1986			
CPUE	43.4 ± 45.3^z	100.4 ± 61.2^z	62.0 ± 13.3^z
Length	76.7 ± 46.6^z	70.2 ± 52.4^z	116.6 ± 72.4^y
N	217	502	310
Species	5.6 ± 2.5^z	11.8 ± 3.2^y	13.4 ± 2.2^y
November 1986			
CPUE	9.0 ± 2.3^z	61.8 ± 16.9^y	36.2 ± 8.8^x
Length	89.5 ± 64.7^z	154.8 ± 79.2^y	117.3 ± 71.6^x
N	45	309	182
Species	3.6 ± 1.5^z	12.2 ± 2.4^y	9.4 ± 2.2^y

Notes:
NP - No plants
IPD - Intermediate plant density
HPD - High plant density
z - Values in rows followed by the same letter are significantly different (Duncan's multiple range test, $P < 0.05$) within each month, separately.

with significantly higher CPUE values at the IPD site were the bay anchovy (August), golden shiner (November), brown bullhead (November), and largemouth bass (November). Species with significantly higher CPUE values at the HPD site were the brown bullhead (August) and largemouth bass (August).

Density

Mean density (number/10m^2) of all species combined ranged from 5.1 $\pm$ 3.6 at the Pend Orielle River to 204.1 + 62.8 at Lake Guntersville (Figure 3). Popnets caught a significantly (P) higher number of fishes at Lake Guntersville than at the the other three locations. Density of all species combined did not differ significantly (P>0.05) between the Pend Orielle River, Potomac River, and Lake Seminole. Density estimates between popnets were most variable at the Potomac River (coefficient of variation, CV = 117 percent), followed by Pend Orielle River (CV = 71 percent), Lake Seminole (CV = 53 percent), and Lake Guntersville (CV = 31 percent).

Table 3
Mean (±SD) Catches of Fishes per 5-min Electroshocking Effort by Fish Species, Plant Density, and Month, Potomac River, 1986

Species	May			August			November		
	NP	IPD	HPD	NP	IPD	HPD	NP	IPD	HPD
Alewife	0	0	0	0.4 ± 0.9^z	5.4 ± 2.7	7.8 ± 5.2	0.4 ± 0.6^z	9.0 ± 6.6	4.6 ± 3.5
Atlantic menhaden	9.8 ± 6.0^z	0.2 ± 0.4	0	12.4 ± 9.3^z	1.2 ± 1.6	0	2.0 ± 1.0	0^z	0.8 ± 1.3
Bay anchovy	6.4 ± 6.4^z	0.2 ± 0.4	0.4 ± 0.8	7.6 ± 12.7	39.8 ± 33.9^z	0.2 ± 0.4	0.2 ± 0.4	1.0 ± 0.7	1.2 ± 1.6
Gizzard shad	0	0.4 ± 0.5	1.0 ± 1.7	0.4 ± 0.9	1.4 ± 2.1	1.2 ± 1.6	0.2 ± 0.4	1.2 ± 1.8	1.8 ± 2.5
Spottail shiner	0	0	5.8 ± 7.7	0.6 ± 1.3	0.4 ± 0.9	3.0 ± 3.1	0	2.0 ± 2.9	0
Golden shiner	0	0	0.4 ± 0.5	0^z	0.8 ± 1.8	2.8 ± 2.8	0	5.2 ± 3.1^z	0.6 ± 0.9
Brown bullhead	0.4 ± 0.9	0	1.2 ± 1.3	0	0.4 ± 0.5	4.6 ± 2.9^z	0	6.0 ± 3.9^z	0.6 ± 0.9
Banded killifish	0	0	0.8 ± 1.3	0^z	2.2 ± 2.3	4.8 ± 2.5	0.2 ± 0.4^z	1.6 ± 1.7	3.4 ± 2.9
Inland silverside	0.8 ± 0.8	0.6 ± 1.3	2.4 ± 2.2	12.6 ± 12.5	21.8 ± 12.8	7.0 ± 4.3	0.4 ± 0.9	2.4 ± 3.3	1.8 ± 1.6
White perch	6.6 ± 6.3	0.2 ± 0.4^z	13.0 ± 12.7	4.4 ± 9.8	10.2 ± 12.1	10.2 ± 3.6	0.2 ± 0.4^z	5.4 ± 4.9	2.0 ± 3.5
Pumpkinseed	0	0	2.2 ± 4.4	0.2 ± 0.4	7.4 ± 11.6	6.2 ± 1.8	0^z	2.6 ± 1.7	7.8 ± 8.5
Bluegill	0	0	0.2 ± 0.4	0^z	2.4 ± 2.3	3.8 ± 2.2	0	0.8 ± 0.8	0.6 ± 1.3
Largemouth bass	0	0	1.0 ± 1.2	0.2 ± 0.4	1.8 ± 1.9	5.4 ± 2.2^z	0	17.4 ± 9.0^z	6.0 ± 2.9
Yellow perch	0	0.4 ± 0.9	3.6 ± 4.8	0^z	1.4 ± 1.7	2.0 ± 1.6	0^z	3.6 ± 3.2	1.6 ± 2.3

Notes:

Each mean is based on five samples. NP = no plants; IPD = intermediate plant density; HPD = high plant density.

z - Values in rows followed by the same letter are significantly different (Duncan's multiple range test, $P < 0.05$) within each month, separately.

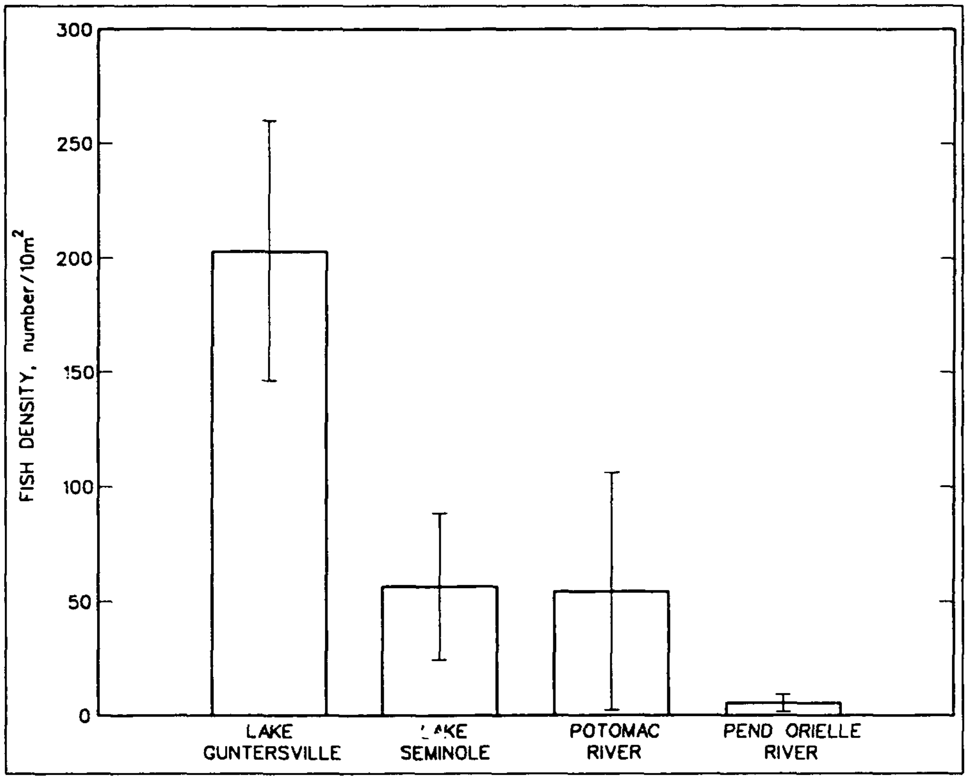


Figure 3. Fish density in submersed aquatic plants at four locations in the United States

Species richness ranged from 7 species at the Pend Orielle to 11 species at the Potomac River and 12 species at Lake Seminole (Table 4). Bluegill comprised approximately 85 percent of the total number of individuals collected at Lake Guntersville. Dominant species at the other locations were coastal shiner, bluegill, and redbreast sunfish at Lake Seminole, banded killifish, inland silverside, and pumpkinseed at the Potomac River, and pumpkinseed at the Pend Orielle River. Mean lengths of fishes were similar between nets regardless of plant density and were generally less than 50 mm.

Feeding Habits

The 10 fishes studied at Lake Seminole (Table 5) represented several trophic guilds, although no species was exclusively herbivorous. Brook silverside and bluegill were midwater and surface film feeders. Over two-thirds of their diets were zooplankton and emergent and terrestrial insects, with zooplankton predominating (Table 6). Bluespotted sunfish and bluefin killifish were midwater and bottom feeders, over one-half of the diet made up of zooplankton and chironomid larvae. The bluefin killifish was more generalized in its food habits, however, feeding to a greater

Table 4
Mean (±SD) Catches of Fishes per 10 m² Popnet Sample

Species	Lake Guntersville	Lake Seminole	Potomac River	Pend Orielle River
American eel	0	0	1.3±1.5	0
Tench	0	0	0	1.0±1.9
Spottail shiner	0	0	0.5±1.2	0
Taillight shiner	0	0.7±1.3	0	0
Coastal shiner	0	10.4±6.8	0	0
Golden shiner	0.4±0.9	0	0	0
Goldfish	0	0	0.7±0.8	0
Longnose sucker	0	0	0	0.1±0.3
Black bullhead	0.3±0.7	0	0	0
Brown bullhead	0	0	0	0.1±0.3
Golden topminnow	0	0.7±0.3	0	0
Starhead topminnow	0	0.3±0.7	0	0
Banded killifish	0	0	14.1±11.9	0
Least killifish	0	0.7±1.3	0	0
Mummichog	0	0	0.6±0.7	0
Bluefin killifish	0	2.7±5.4	0	0
Mosquitofish	0	3.7±7.4	0	0
Brook silverside	16.9±16.1	0.6±0.7	0	0
Inland silverside	0	0	13.3±19.7	0
White perch	0	0	6.3±10.2	0
Warmouth	4.0±4.9	0	0	0
Pumkinseed	0	0	15.8±23.9	3.4±2.1
Bluegill	172.2±51.9	10.8±9.3	1.8±1.6	0
Longear sunfish	1.8±4.0	0	0	0
Redear sunfish	8.2±12.3	4.8±5.0	0	0
Redbreast sunfish	0	20.0±40.0	0	0
Largemouth bass	0.9±1.4	2.0±3.2	0	0.1±0.3
Black crappie	0	0	0	0.1±0.3
Tesellated darter	0	0	0.2±0.4	0
Yellow perch	0	0	0.2±0.4	0.3±0.5

Table 5
Species Abbreviation of the 10 Most Abundant Fishes Collected in Lake Seminole

Species	Common Name	Ranked Abundance	Species Abbreviation
Notropis petersoni	Coastal shiner	5	PETE
Fundulus chrysotus	Golden topminnow	8	CHRY
Fundulus escambia	Eastern starhead topminnow	10	ESCA
Lucania goodei	Bluefin killifish	3	GOOD
Heterandria formosa	Least killifish	9	FORM
Labidesthes sicculus	Brook silverside	1	SICC
Enneacanthus gloriosus	Bluespotted sunfish	4	GLOR
Lepomis macrochirus	Bluegill sunfish	2	MACR
Lepomis microlophus	Redear sunfish	7	MICR
Micropterus salmoides	Largemouth bass	6	SALM

extent on benthos than did bluespotted sunfish and feeding on several foods that made up only marginal portions of the diet of bluespotted sunfish (i.e., trichoptera, terrestrial invertebrates, and plants). The coastal shiner and least killifish were omnivores, feeding to a greater extent on plants (over 20 percent of the diet) than did the other species (less than 7 percent of the diet). The golden topminnow was a benthivore, with more than two-thirds of its diet made up of larval chironomids and ostracods. The redear sunfish was a benthivore; molluscs and larval chironomids (in near equal proportions) made up more than 75 percent of its diet. The eastern starhead topminnow was a specialized surface film feeder, with emergent and terrestrial insects making up 80 percent of its diet. The largemouth bass was mainly piscivorous; 40 percent of its prey were fishes, but no single taxon or prey group dominated the remainder of its diet.

Intraspecific similarity in diets between the two habitats was not high (PSI < 0.750) for any species, but there was substantial variation among the fishes. Moderate values (PSI = 0.564-0.604) were obtained for bluefin killifish, brook silversides, and largemouth bass and low values (PSI < 0.350) for the remaining species. The diet of redear sunfish showed the lowest degree of similarity between habitats (PSI = 0.177).

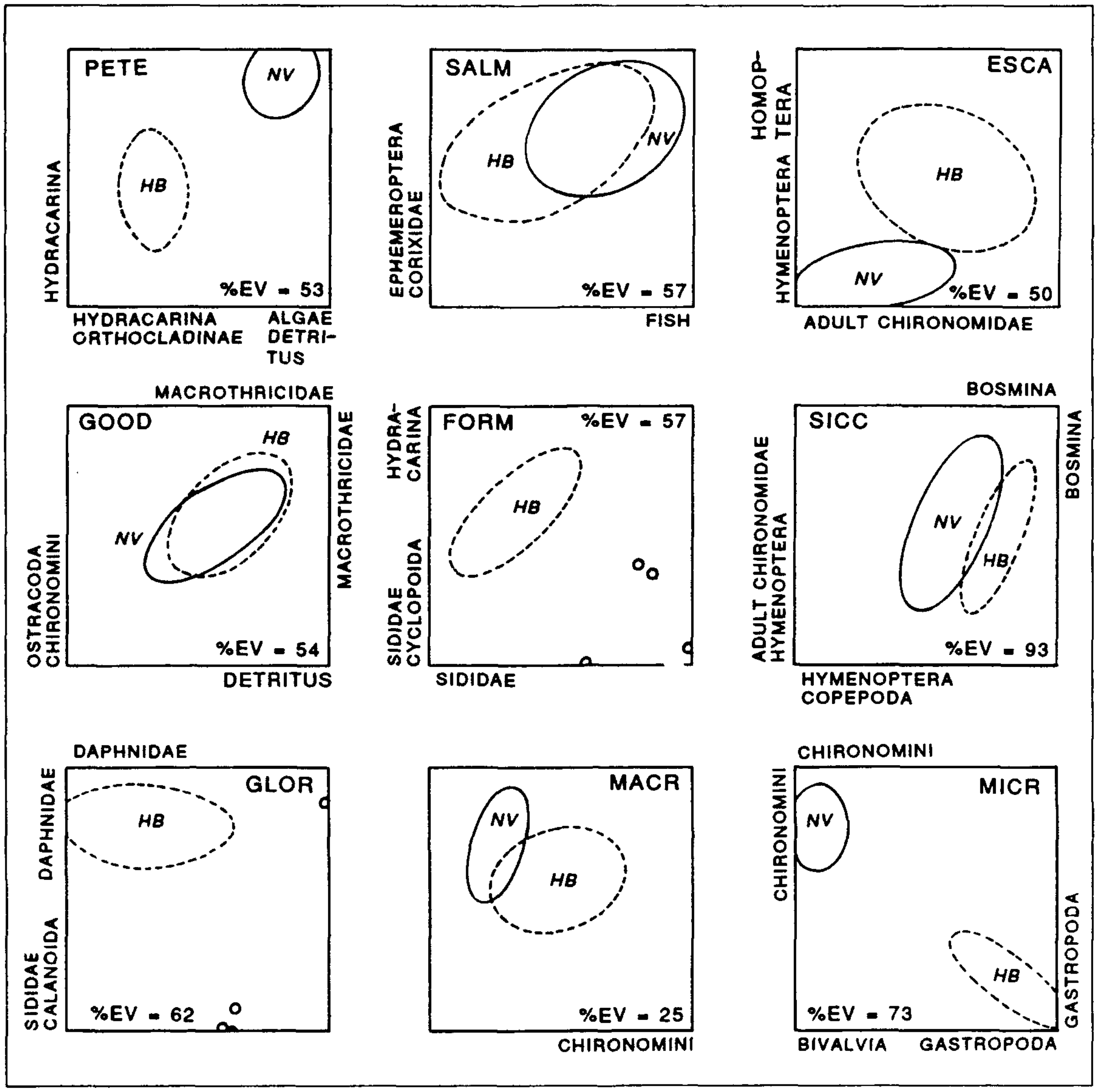
PCA indicated that intraspecific variability in diet composition was comparable at the two sites for most species (Figure 4). Paired ellipses could not be created reliably for golden topminnow, least killifish, and bluespotted sunfish due to low sample sizes (n = 8), but those generated for the other seven species were not greatly disparate in size (i.e., ellipse

Table 6
Food Habits of 10 Species of Fishes from Lake Seminole, Florida-Georgia

Sample size	PETE 15-15	CHRY 4-7	ESCA 10-11	GOOD 15-15	FORM 4-15	SICC 15-15	GLOR 4-15	MACR 14-15	MICR 15-15	SALM 15-15
Plant Foods										
Algal filaments	14		T	T	8			1	1	
Diatoms					5					
Desmids				T	4					
Macrophytes		1	1		1			2	1	7
Detritus	21		T	2	5	T		2	T	
Aquatic Invertebrates										
Gastropoda		2		1				2	21	
Bivalvia									17	
Hydracarina	32		1	1	14	1	2	4		
Oribatidae	1	1	5	6	T	T		1		2
Amphipoda		1	1	T				1	7	
Ostracoda		43		12	2		1	2	1	
Copepoda			T	4	12	9	16	2		
Cladocera	1		3	32	34	60	65	35		
Ephemeroptera	6	4	T	1	T		1	2	1	15
Odonata		1		T			1		1	9
Hemiptera			1	T						10
Coleoptera		11	1	T			1	1		
Trichoptera		8	T	8			1	1	3	3
Diptera (misc)			6	1	T	T	1	T	4	
Chironomidae										
Pupae		1	39	1		T		1	T	2
Largae	14	24	1	21	7	1	8	12	38	5
Other			2	1	6	1		T	1	2
Fish, Fish eggs				T			T	1	1	40
Terrestrial Invertebrates										
Homoptera			9							
Hymenoptera	1		5			1		7		
Diptera (misc)			5					1		
Chironomidae	7		23			25	T	4		
Other	2	3	5	8	T	T	1	17	1	2
Total number of prey	112	140	343	488	211	1389	279	670	285	58

Notes:
Species abbreviations from Table 5.
Numbers represent numerical percentage of prey (T = trace).
Sample sizes are for collections made at nonvegetated and vegetated stations, respectively.

size differences were substantially less than an order of magnitude). There was a trend for ellipse area to be greater for fishes collected in hydrilla, though, suggesting a tendency for increased intraspecific variability in diet composition for fishes in vegetation. Only brook silverside exhibited a larger ellipse for the nonvegegtated site. The remaining six species had larger ellipses (point spread) in the hydrilla collections. Ellipse size disparity was minimal (<10 percent) for bluefin killifish and redear sunfish, moderate (approximately 45 percent) for coastal shiner and largemouth bass, and greatest (>100 percent) for eastern starhead topminnow and bluegill. PCA ellipse separation was usually consistent with the PSI values. PSI values were low (<0.300) for several species and this was reflected by ellipses that were well-separated (e.g., coastal shiner and



Notes:
Ellipses based on point spread of individual fishes within each habitat (outside and inside a hydrilla bed).
Prey taxa indicated were significantly correlated with PC coordinates along that axis; positively correlated taxa listed at right and negatively correlated taxa listed at left.

Figure 4. Principal component analysis of diets of fishes collected in Lake Seminole

redear sunfish) or overlapped only marginally (e.g., eastern starhead topminnow and bluegill). However, when PSI values were higher, but within a small range (i.e., 0.564-0.604), ellipses overlapped marginally (brook silverside), moderately (largemouth bass), or almost completely (bluefin killifish). Complete agreement between the two measures (PCA and PSI) would occur only if prey numbers and frequencies were equivalent between habitats and if low-frequency prey did not make up an important percentage of the diet.

Some prey (e.g., bosminidae, bivalves) were consumed preferentially by a single species of fish, but no taxon was eaten in large numbers by all species (Table 6). Of 58 prey types eaten, 17 showed significant correlations with PC I or II (Figure 4). Larval chironomini were important to four species (golden topminnow, bluefin killifish, bluegill, redear sunfish) and copepods to three species (least killifish, brook silverside, and bluespotted sunfish). Other invertebrate taxa (e.g., larval orthocladinae, hydracarina, homoptera, various cladocera) showed significant correlations with PC loadings for only 1 or 2 species of fish.

Habitat-associated differences in diet varied with each species of fish, although several species in hydrilla fed on larger numbers of hydracarina and lower numbers of copepoda and terrestrial insects than did conspecifics at the nonvegetated site (Figure 4). Coastal shiners collected at the vegetated site fed less frequently on algae than did individuals from the nonvegetated site and more frequently on hydracarina and larval orthocladinae. Eastern starhead topminnow at the vegetated site ate fewer adult chironomids and hymenoptera, and consumed more homoptera. Least killifish, brook silverside, and bluespotted sunfish all consumed larger numbers of copepods and cladocera at the nonvegegtated site than at the vegetated station. Least killifish and bluespotted sunfish ate over four times as many sidids and daphnids at the vegetated site, respectively, than did conspecifics from the nonvegetated site. Mean numbers of bosminids eaten by brook silverside were higher at the nonvegetated station (35.47/individual) compared to the vegetated site (17.93/individual), although this appears contradictory to PCA results that indicated greater bosminid utilization at the vegetated site. Bosminids occurred more frequently and in less variable (albeit lower) numbers in the diets of hydrilla-collected brook silverside (C.V. = 83 percent) than in those individuals from the nonvegetated site (C.V. = 129 percent). Brook silverside at the nonvegetated station also consumed significantly lower numbers of adult chironomids (5.27/individual) than those fishes in the hydrilla bed (17.87/individual)(test (t) = 2.74, degrees of freedom (d.f.) = 29, probability (p) < 0.05). Bluegill ate large numbers of hymenoptera and low numbers of larval chironomini at the nonvegetated site; this pattern was reversed, however, at the vegetated site where low numbers of hymenoptera and high numbers of chironomini (2.20/individual) were eaten. Consumption of several other prey taxa by bluegill was also different in vegetation, but was not significantly correlated with principal components: plant foods (1.46/individual versus 0.66/individual), sidid cladocera (12.60/individual versus 0.00/individual), and hydracarina (1.67/individual versus 0.27/individual).

Three of the remaining four species ate fewer larval chironomini in the hydrilla bed than at the nonvegetated station (Figure 4). Although only a few golden topminnow were collected from each habitat, there was an indication that individuals from the hydrilla bed were eating fewer chironomini (1.0/individual versus 2.3/individual) and larger numbers of other benthic prey (i.e., ostracods, beetles, and caenid mayflies). Major prey of bluefin killifish at the nonvegetated site were also important

dietary components for individuals collected in the hydrilla bed; differences in prey numbers for taxa correlated with principal components (i.e., macrothricid cladocera, larval chironomini, and detritus) were not greatly disparate, hence there was little separation of PC ellipses. There were some other differences in food habits that were not associated with PC axes that accounted for moderate similarity in diet between habitats. Bluefin killifish at the nonvegetated station ate large numbers of larval hydroptilid caddisflies (2.27/individual) while individuals collected in the hydrilla bed ate none. Redear sunfish that occurred at the nonvegetated site ate large numbers of bivalve molluscs (3.27/individual) and chironomini (5.60/individual) but smaller numbers of snails (0.60/individual); in vegetation, though, this species ate large numbers of snails (3.47/individual), few chironomini (0.20/individual), and no bivalves.

Diet partitioning among species was pronounced in both habitats (Figure 5). Of 90 pairwise comparisons among the 10 species, 73 resulted in a PSI less than 0.200, and none resulted in overlaps greater than 0.500. Species pairs exhibiting even slight similarity in diet (PSI>0.250) were relatively uncommon (8/90). Coastal shiner, brook silverside, and largemouth bass did not exhibit moderate overlap with any species in either habitat, probably due to their distinctive specializations on water mites, cladocera, and fish, respectively (Table 6). Only two instances of overlaps greater than 0.400 occurred: golden topminnow and redear sunfish both consumed large portions of larval chironomids in areas without vegetation; least killifish and bluegill both ate substantial numbers of sidid cladocera in vegetation.

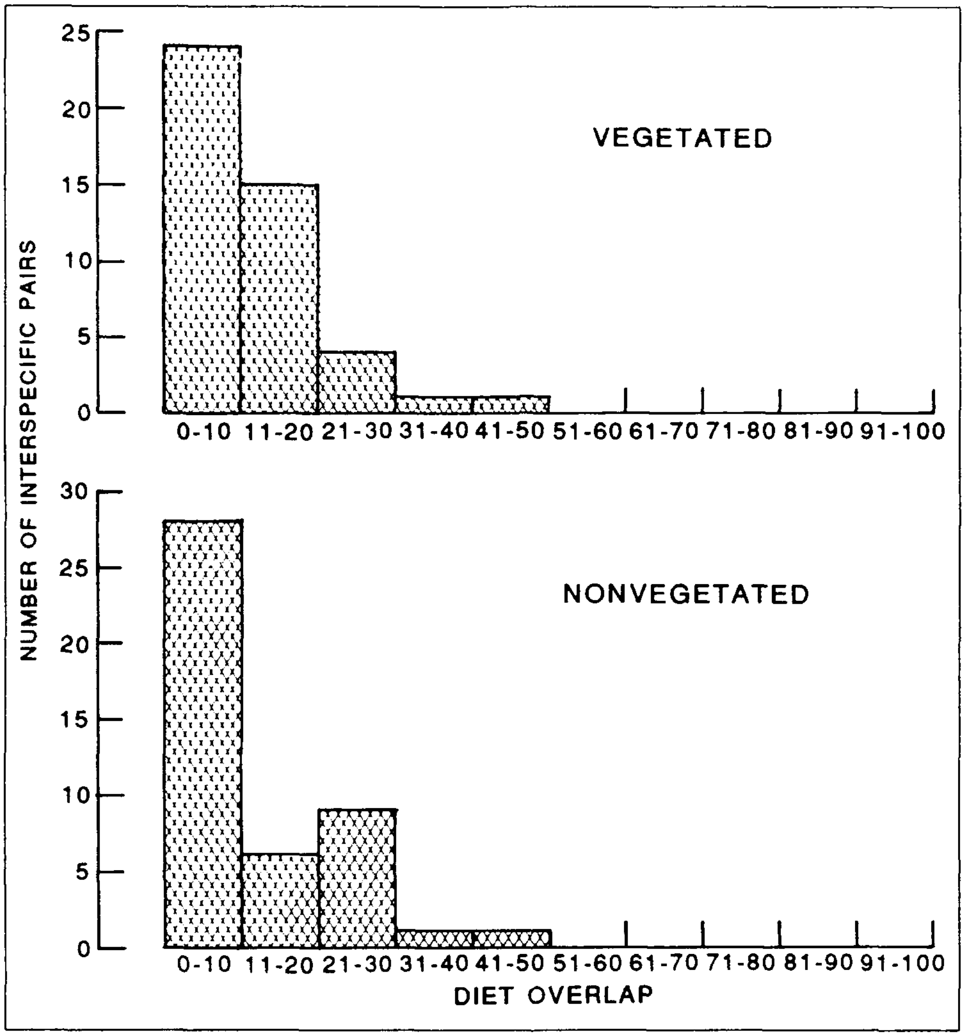


Figure 5. Frequency distribution of interspecific overlaps among Lake Seminole fishes

5 Discussion

Seasonal Distribution and Abundance

The seasonal change in density and species composition of aquatic plants causes a transition in the spatial and temporal distribution of fishes. In the spring when plant density is relatively low in the Potomac River, fish abundance was highest in areas without plants because of the occurrence of anadromous, pelagic-oriented species (alewife, Atlantic menhaden, and bay anchovy) or in areas with mature stands of Eurasian watermiifoil (HPD site), rather than emerging short stands of hydrilla (IPD site). During the spring, fishes tend to associate with aquatic plants that overwinter or emerge early from the substrate for food and cover and disperse to the more established macrophyte beds in the summer and fall (Hall and Werner 1977).

Once the plant community has reached its maximum density in the summer, plants capable of establishing dense stands, such as hydrilla, can occupy the entire water column and have the potential of decreasing fish movement and foraging efficiency. Therefore, fish abundance and condition are often higher in areas of intermediate levels of structural complexity, particularly for piscivorous species (Crowder and Cooper 1979; Colle and Shireman 1980; Savino and Stein 1982; Durocher, Provine, and Kraai 1984; Wiley et al. 1984). On a community level, our study in the Potomac River tends to support this conclusion. During the August and November sampling periods, intermediate densities of submersed aquatic plants usually contained more species and numbers of fishes than areas having dense growths.

Although the abundance of fishes was higher in areas with intermediate densities of plants during the summer and early fall, certain species or groups of species appeared to prefer areas with high plant densities. Based on electroshocking, pumpkinseeds were usually collected within the mass of dense vegetation. Piscivorous fishes (largemouth bass and yellow perch) were commonly observed occupying small "holes" devoid of plants in dense vegetation and apparently modifying foraging tactics from an active pursuit of prey to ambush, thus minimizing energy costs required for prey capture (Savino and Stein 1982). The banded killifish,

American eel, and brown bullhead were associated with other distinct niches formed by dense plant beds. The banded killifish was commonly observed swimming directly over the plants at high tide and the American eel and brown bullhead were collected along the bottom underneath a dense canopy of hydrilla where plant biomass is reduced. Therefore, many fishes will associate with either the water surface immediately above the plants, the periphery of the dense stands ("edge effect"), "holes" formed in the plant beds, or the bottom directly below dense canopy formations to utilize both open and structurally complex areas for foraging and predator avoidance.

Average lengths of fishes may be lower with increasing plant density. Barnett and Schneider (1974) reported that fishes were usually less than 150 mm long and small fishes, such as *Heterandria formosa, Lucania goodei, Gambusia affinis*, and juvenile centrarchids were the dominant species in dense aquatic plant communities, while larger, piscivorous fishes were more common at the periphery of the plant beds. However, lower mean lengths of fishes with increasing plant density was not evident in our study. In August, overall fish length was significantly higher in areas with high plant density, whereas in November, fish length was significantly higher in areas with intermediate density. Hall and Werner (1977) and Mittelbach (1984) found that sunfish (bluegill, pumpkinseed), less than 80 mm in length, associate with dense aquatic plants to avoid predators, and their diets were quite similar, but as they grow larger and change feeding preferences, they move above or away from plants. Most centrarchids collected in plant beds (intermediate and high density) in the Potomac River were juveniles and comprised one of the major groups of fishes collected throughout the study. As these fishes grow during the summer, they become less vulnerable to predators and may move to areas of lower plant density to achieve higher feeding rates (Mittelbach 1981).

Density

Aquatic macrophytes can contribute to an increase in fish abundance, particularly in areas once devoid of any substantial amounts of cover. For example, Borawa et al. (1978) found that fish density increased from approximately 1,000 to more than 15,000 fishes/hectare after Eurasian watermilfoil became established in Currituck Sound. In our study, mean fish density ranged from 5,000 to 204,000 fishes/hectare in areas with plants. Fish density was considerably lower in areas without plants. High fish density values have also been reported by other researchers. Fish density ranged from 13,000-205,000 fishes/hectare in areas with submersed aquatic plants in Orange Lake, Florida (Shireman, Colle, and DuRant 1981; Haller, Shireman, and DuRant 1980) , and up to 86,000- 2,500,000 fishes/hectare in several lentic locations in central Florida (Barnett and Schneider 1974).

Geographical differences in fish density and species composition was pronounced. In the Pend Orielle, fish density was substantially lower than other locations sampled. This is probably due to prolonged winters resulting in shorter reproduction and growing periods of fishes. Juvenile pumkinseed sunfish was the most common fish collected in the plants, indicating that sunfishes are usually the dominant or codominant group of species found in most vegetated areas in the United States.

Fish density at Lake Seminole was similar to the Potomac River. Higher fish densities may occur in isolated areas at Lake Seminole, but within large (>100 acres) dense hydrilla beds, fish density was comparably low. This may be due to poor water quality (low dissolved oxygen (D.O.) high pH) that typically occur in vegetated areas. Water quality measurements taken during fish sampling showed that D.O. ranges from 2.0 mg/l to saturation, and pH can rise to over 9.0 in the afternoon. Therefore, diel fluctuations in water quality may contribute to low fish density in areas with submersed aquatic plants.

Fish density at the Potomac River was intermediate, but compared to nonvegetated areas where fish abundance was low as determined by electroshocking, the establishment of aquatic plants in the Potomac River has a positive influence on the abundance of fishes, particularly juvenile sportfishes (largemouth bass, yellow perch, pumpkinseed). For example, over 300 largemouth bass were collected in areas with aquatic plants, while only one individual of this species was collected in areas without plants. Considering all fish species collectively, up to seven times more fishes were collected in areas with plants. Fishes in areas without plants were pelagic (clupeids, anchovies, and silversides), whereas these and cover-oriented species (pumpkinseed, largemouth bass, yellow perch, brown bullhead) were abundant in areas with plants.

Lake Guntersville had the highest fish density, and the community was dominated by juvenile bluegill. High fish densities indicate that aquatic plants provide the necessary cover and food to promote high survival of sunfishes compared to other locations sampled. When rivers with deep channels, such as Lake Guntersville and Potomac River, prevent Eurasian watermilfoil and other fast-growing plants from occupying the entire waterbody, drastic changes in the physiochemical environment that results from total coverage of a waterbody are minimized. In addition, annual senescence of the plant community results in a gradual reduction in refuge for small fishes, giving piscivorous fishes an opportunity to feed more efficiently before forage fish abundance diminishes during the winter. This would lead to a potential increase in sport fish recruitment while reducing the likelihood of a stunted fish population.

Fish density estimates in aquatic plants are inherently variable due to sampling techniques, plant density, and patchy fish distribution. However, the popnets used in this study can easily be deployed in replicate numbers to account for this variability common in structurally complex habitats. Variability between individual popnet collections were high for

each site indicating patchy distributions within the plant beds. In addition, the popnets reduce the potential bias of underestimating fish abundance that is associated with techniques that require the collection of stunned (electrofishing) or dead (rotenone) fish with a dip net in dense plant beds, although the efficiency of the popnets in collecting more mobile fish in vegetated areas, such as shad and black bass, remains untested. However, Larson, Johnson, and Lynch (1986) reported that the sampling efficiency of the popnets was near 100 percent and can accurately sample the entire fish assemblage around artificial structure. A similar method was used by Freeman, Greening, and Oliver (1984) who sampled fishes in areas with aquatic plants by using a drop trap (1 m^2) from which 90 percent of tagged fishes were recovered.

Feeding Habits

The diets of Lake Seminole fishes were comparable with previously published food habits for those species, with two exceptions. Diet information is not yet available for the recently described eastern starhead topminnow, and only limited information is available on the food habits of lentic coastal shiner. Davis and Louder (1971) reported that coastal shiner fed primarily on entomostraca. Individuals in Lake Seminole fed chiefly on hydracarina, detritus, larval chironomids, and filamentous algae. Davis and Louder also reported algae and detritus from the gut contents of coastal shiner but suggested that plant materials were consumed incidentally and were of negligible nutritional value.

Several studies have surveyed food habits for large assemblages of fishes (e.g., Hunt 1952, Flemer and Woolcott 1966, Keast and Webb 1966, Keast 1985), but these have focused primarily on interspecific resource partitioning and have not emphasized small-scale variations in diet, such as those existing among different habitats. Investigators have noted substantial shifts in diet composition for some species coinciding with changes in habitat, but these observations have been restricted to one to three species (Cahn 1927, Hall et al. 1979, Werner and Hall 1979, Crowder and Cooper 1982). An assemblage-level evaluation and community-level generalization regarding degree of diet change between habitat types is lacking. Our results suggest that diet shifts can be substantial between habitats (i.e., PSI < 60 percent) within an entire assemblage, irrespective of trophic guilds and degree of dietary specialization.

Sidid cladocera tend to be less abundant in open water than in vegetation (Quade 1969, Fairchild 1981). At the nonvegetated site, least killifish and bluegill specialized on benthic invertebrates and daphnid cladocera, but in the hydrilla bed, both species fed on sidids more than any other prey. In contrast to sidids, bosminid cladocera are more abundant in open water than in vegetation (Quade 1969, Fairchild 1981). This was reflected in the diet of the specialized predator, brook silverside; bosminids were consumed more frequently in open water. In the case of brook silverside,

however, factors other than prey availability may influence their diet composition. This species is morphologically specialized for open water swimming and feeding (Keast and Webb 1966) and is almost always more abundant in open waters than in vegetation (Goin 1943; Reid 1950; Ager 1971; Barnett, 1972; Guillory, Jones, and Rebel 1979). Also, silversides select bosminids by visual discrimination of the cladoceran's eyespot (Zaret and Kerfoot 1975). It seems reasonable to assume that physical impediments (to swimming) and the visual impediments (to prey detection) presented by the hydrilla resulted in lower feeding efficiency of some individuals. This is supported by our estimates of gut fullness of brook silverside which were significantly higher in open water specimens (74 percent full) than in specimens from the hydrilla bed (57 percent full)($t = 2.634$, d.f. = 28; $p < 0.05$).

Habitat-associated differences in the diet of Lake Seminole fishes may also be influenced by intraspecific interactions. Larger group sizes have impacted feeding activity probably through passive information exchange (Pitcher, Magurran, and Winfield 1982) and reduced vigilance (Pitcher and Magurran 1983). If larger populations of fish are less sensitive to predator effects (Pitcher, Magurran, Winfield 1982) and to interspecific competitive restraints (Werner and Hall, 1979), and if they experience greater degrees of intraspecific "information exchange" (Pitcher, Magurran, and Winfield 1982), they should also exhibit higher similarity in diets between habitats. This speculation is supported by our observations. Among the nine invertivorous fishes, there is a significant positive correlation between abundance (total numbers of fishes collected) and similarity of diets (PSI) between stations (correlation coefficient (r) = 0.666, sample size (N) = 9, probability (p) = 0.05). Such a relationship underscores the importance, and the difficulty, of evaluating multiple factors which may be responsible for small-scale changes in the diet of fishes.

Aquatic plants provide an important forage base to fishes and can influence their distribution and condition (Colle and Shireman 1980; Hall and Werner 1977; Holland and Huston 1984). Although this study indicates that many fish species alter feeding habits when they encounter aquatic plants, their trophic dynamics are not yet fully understood. However, as new information on this subject becomes available to aquatic plant managers, the functional relationship between plants and the diet of fish can be considered when choosing the appropriate level of control.

6 Conclusions and Recommendations

The presence of aquatic plants influences the relative abundance of fishes in littoral areas. Fish abundance is lowest in the winter and spring when plant density is low. During the summer and fall when plants reach their maximum density, fish abundance is highest in areas with plants, usually because of the high abundance of juvenile centrarchids. Within the plant bed, however, fish abundance and condition are often higher in areas of intermediate levels of structural complexity, particularly for piscivorous species.

Aquatic plant beds form distinct habitats, creating a heterogeneous environment for fishes. Fishes will associate with the water surface immediately above the plants, the periphery of the dense stands ("edge effect"), "holes" formed in the plant beds, or the bottom directly below dense canopy formations to utilize both open and structurally complex areas for foraging and predator avoidance.

Aquatic macrophytes can contribute to an increase in fish abundance, particularly in areas once devoid of any substantial amounts of cover. In this study, mean fish density ranged from 5,000 to 204,000 fishes/hectare in areas with plants, which is consistent with other studies that measured fish density in aquatic plant beds. However, geographical differences in fish density and species composition was pronounced. Fish density estimates at all sites were extremely variable, indicating patchy distribution within the plant bed. Fish may exhibit substantial diel movement within the plant bed to avoid low D.O. in the morning and high pH in the afternoon.

Diet shifts can be substantial between habitats (i.e., PSI > 40 percent) within an entire assemblage, irrespective of trophic guilds and degree of dietary specialization. Substantial habitat-associated differences in diet existed for all species, probably attributable to differences in invertebrate availabilities rather than structure-induced changes in feeding behavior or feeding efficiencies.

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